

Agassiz, Darwin, Huxley, and the fossil record of teleost fishes

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Synopsis

Darwin cited teleost fishes as the best documented instance of the sudden appearance of a major group. This paper reviews the work of Darwin's contemporaries, particularly Louis Agassiz and T. H. Huxley, on the composition, characterization, and mode and time of appearance of the teleosts, and compares their opinions with views held today. It seems that modern ideas differ little from those of Darwin and his contemporaries. The problems which occupied them, and are still with us today, are principally problems of systematics, or discovering the natural system, problems that seem hardly to have been affected, and certainly not solved, by new discoveries of fossils and a century of progress in palaeontology.

Introduction

In the first edition of *The Origin of Species*, under the heading 'On the sudden appearance of whole groups of allied species', Darwin wrote (1859: 305): 'The case most frequently insisted on by palaeontologists . . . is that of the teleostean fishes, low down in the Chalk period. This group includes the large majority of existing species. Lately, Professor Pictet has carried their existence one sub-stage further back; and some palaeontologists believe that certain much older fishes . . . are really teleostean. Assuming, however, that the whole of them did appear, as Agassiz believes, at the commencement of the chalk formation, the fact would certainly be highly remarkable but I cannot see that it would be an insuperable difficulty on my theory, unless it could likewise be shown that the species of this group appeared suddenly and simultaneously throughout the world at this same period.' Darwin goes on to note that 'hardly any fossil-fish are known from south of the equator' and proposes that teleosts might have developed within some enclosed basin, and dispersed rapidly thence when climatic or geographic change gave access to the open sea. In the sixth edition of *The Origin* (1872) Darwin amplified this passage by adding 'certain Jurassic and Triassic forms are now commonly admitted to be teleostean; and even some palaeozoic forms have thus been classified by one high authority'. This high authority was T. H. Huxley (1861), and 'now commonly admitted' amplifies the original reference to Pictet.

The aim of this paper is to discuss the fossil record of teleosts as it illuminates this passage from Darwin. Did teleosts first appear in the Cretaceous (Agassiz) or the Devonian (Huxley)? Is their time and mode of appearance a reflection of the imperfection of the geological record (the title of Darwin's chapter), or of the beliefs of palaeontologists (as his text suggests)? Could the teleosts, and their fossil record, be 'an insuperable difficulty' for Darwin's theory? There are three aspects to consider: the characterization of the teleosts, their composition and age, and their implications for Darwin's theory. These aspects are not independent, for the composition and age of the teleosts are largely dependent on the characterization of the group, and the implications of fossil teleosts – the general principles induced or deduced from their record – may vary with the age and composition of the group.

which Müller showed to be teleosts by his criteria of soft anatomy (two valves in the conus arteriosus, no optic chiasma).

The problem of characterizing teleosts by osteological characters, applicable in fossils, was one which occupied pre-Darwinian palaeontologists (see Patterson, 1977, for a review). The solution which has best withstood the test of time is Heckel's (1850): teleosts are those fishes in which the caudal end of the notochord is roofed by uroneurals, or enclosed in a terminal half-centrum. This solution was not universally adopted by mid-nineteenth century palaeontologists because of their respect for Agassiz' scale characters. In fossils, Agassiz identified enamelled scales not by study of thin sections, but by 'l'oeil nu' (1844, 1 : 74). His Ganoidei included, as well as living teleosts like catfishes and tetraodontiforms, several Jurassic genera (including fishes now named *Leptolepis*, *Tharsis*, *Thrissops*, *Allothrissops*, *Anaethalion*) with thin, flexible scales. Müller (1846 : 520) examined scales of *Leptolepis* and confirmed the presence of enamel. It was more than a century before Heckel's caudal skeleton characters were revised and applied to fossil teleosts (Nybelin 1963), and it was as long before Agassiz' and Müller's authoritative statements about enamel on the scales of *Leptolepis*, etc., were shown to be wrong (Schultze 1966). Fishes with uroneurals may have cycloid scales, ganoid scales, or a mixture of the two (Schultze 1966, Nybelin 1966, Patterson 1968a). Müller's prediction that Agassiz' classification, because based on a single character, 'might prove rather an artificial than natural system' (Müller 1846 : 505) has been borne out. Yet Müller's definition of the teleosts (two valves in the conus) and Heckel's (uroneurals) also rely on single characters, as Agassiz (1858) pointed out. What, then, does 'natural' mean? Are single character classifications always suspect? The distinction between 'artificial' and 'natural' classifications goes back to antiquity (Russell 1916, Bather 1927, Simpson 1961), and the meaning of those terms has changed with underlying theory. Yet a common thread running through all discussions is that a natural classification is one conforming with a large number of characters, whereas an artificial classification is a key or identification system, relying on single characters. The difference between Agassiz' scale character (enamel) and Heckel's tail character (uroneurals) agrees with this distinction. For Agassiz' criterion, a grouping of all those fishes with enamelled scales, opposed to a group of all those with unenamelled scales, cuts across the groups formed by many other characters, and conforms with none. In phylogenetic terms, the first group (enamelled) would be paraphyletic, and the second (unenamelled) polyphyletic. Heckel's criterion, grouping all those fishes with uroneurals or a terminal half-centrum, agrees with Müller's (two valves) not because both criteria define the same group, but because Heckel's group includes Müller's as a subset (some fishes with uroneurals, such as *Albula* and *Megalops*, have two pairs of valves; Bertin 1958). But that cannot be the whole story, for Müller's group is also a subset of Agassiz' Cycloidei and Ctenoidei: all fishes with two valves in the conus have cycloid or ctenoid scales (some with cycloid scales, such as *Amia*, have three sets of valves). Why, then, are Agassiz' groups not natural? The answer involves further characters. For instance, additional osteological characters now thought to be characteristic of teleosts are epineural bones, a supraoccipital bone extending forwards into the otic region, and a myodome extending into the basioccipital (Patterson 1973). All these features occur in fishes with ganoid and with cycloid scales, but all occur only in fishes with uroneurals (i.e., as subsets of that group). When such conditions are met, probabilistic arguments (Wilson 1965, Patterson 1981) can be used to show that the congruence of the characters is unlikely to be due to chance, and the groups so formed may be regarded as natural, or, in phylogenetic terms, as monophyletic. Intuitive use of such arguments presumably influenced Agassiz, and by 1857 he had given up his classification of the teleosts.

Composition and age of the teleosts

Since Agassiz' and Darwin's time, the number of accepted fossil teleosts, and of teleost

groups with fossil members, has grown enormously. This accretion has two sources: first, finds of new fossils, and second, inclusion of previously known fossils through changed characterization of the teleosts. In numerical terms (number of specimens, or of named species or higher taxa) the first of these must predominate; but in terms of general principles, or patterns, which occupied Agassiz and Darwin, the second is probably more important. For although the density of sampling and its geographic range have increased, the temporal pattern of the samples has altered little.

Agassiz' conclusion, that teleosts were unknown before the Cretaceous (Fig. 1) was not altered by inclusion in the teleosts of those groups (catfishes, etc.) which Müller showed were wrongly placed in the Ganoidei, for none of these had, or has, a fossil record extending beyond the Cretaceous. The opinions cited by Darwin (1859, 1872), whether teleosts first appeared in the Cretaceous, Jurassic, Triassic or Palaeozoic, concerned the characterization of the group, and whether various other fishes, known to Agassiz and included by him in the Ganoidei, were teleosts or not. According to Heckel (1850), who characterized teleosts by the presence of uroneurals, the Jurassic genera *Leptolepis*, *Thrissops*, *Tharsis* and *Anaethalion*, ganoids to Agassiz, were teleosts; teleosts therefore first appeared in the Lower Jurassic. According to Pictet (1854), who accepted Agassiz' identification of enamel on the scales of these Jurassic fishes, and the significance of that character, teleosts first appeared in the Cretaceous. But by 1858, Pictet had worked on newly-discovered teleosts from the Lower Cretaceous (Agassiz knew little or nothing from those strata), and found that their caudal skeleton was constituted in the same way as those of Jurassic leptolepids. Pictet believed that one of his Lower Cretaceous teleost genera had enamelled scales ('qui peut bien être un simple modification de la surface par la fossilisation') whereas the other lacked enamel. Therefore enamel could not be 'un caractère de premier ordre'. And Pictet agreed that the Jurassic fishes placed in the Teleostei by Heckel were true teleosts. I assume that Darwin (1859) cited Pictet's opinion from this 1858 paper.

In 1861 Huxley sought to extend the fossil record of teleosts into the Palaeozoic, by a detailed comparison of the dermal bones of the skull and shoulder girdle of the Devonian arthrodire *Coccosteus* and the Recent catfish *Clarias*. According to Woodward (1891 : vi), Huxley's error resulted 'from too narrow a conception of the limits within which certain minor skeletal characters may occur', or in more general terms (1891 : v) a 'tendency to interpret the past by a rigorous comparison with the present'. My own view is that Huxley's error lay in denying the generality of the osteological features used by Heckel and others to define the Teleostei and teleostean subgroups. For instance, Günther's (1859 : 1) definition of the Teleostei reads (in part) 'Fishes with ossified skeleton and completely separated vertebrae; the posterior end of the vertebral column either bony, or covered with bony plates'. In proposing *Coccosteus* (which lacks these features) as a teleost, Huxley denies that they are teleostean features, and denies that the catfish caudal skeleton (which Heckel found to be of the type termed 'steganochordal' by Huxley in 1859) is characteristic of that group. In short, Huxley seems to adopt a method which neglects the orderly hierarchy of homologous characters discovered by Müller, Heckel and others. Huxley's conclusion, that *Coccosteus* might be a teleost, found virtually no support: according to Woodward (1891 : vi), Newberry (1889) alone agreed.

In 1866, Pictet & Humbert published a monograph on the Cretaceous fishes of the Lebanon, a fauna known since the thirteenth century, but poorly represented in European collections; Agassiz (1833-44) listed only eight species. Darwin, writing to Lyell in 1866, called Pictet & Humbert's work 'a capital paper . . . It is capital in relation to modification of species; I would not wish for more confirmatory facts, though there is no direct allusion to the modification of species' (Darwin & Seward 1903, 2 : 160). Darwin was referring to the English abstract of Pictet & Humbert (1866*b*), and no doubt what pleased him most in this translation was statements like 'Salmones and Clupeae . . . [are] actually the descendants of the Jurassic teleosteans [*Leptolepis*, *Tharsis*, etc.] . . . and may be regarded as . . . the trunk of the genealogical tree'. And that the salmones and herrings (Clupeae) 'are also those that have the longest pedigrees'. 'Descendants' in the first quotation is 'continuateurs' (successors), a

more Agassizian word, in the original, but 'pedigrees' in the second quote is 'aïeux' (ancestry) in the original. Pictet & Humbert go on to discuss Agassiz' group *Halecoïdes* (salmon, herring, etc.) in Owenian terms, as representing the archetype of teleosts, in addition to containing the only Jurassic forms. I suppose that the 'Jurassic' part of Darwin's (1872) addition to the *Origin* ('certain Jurassic and Triassic forms are now commonly admitted to be teleostean') comes from his reading of Pictet & Humbert. As for the source of the 'Triassic' part, one cannot be sure but there seem to be only two possibilities. The first is Lütken (1869, English translation 1871), who included the Triassic *Belonorhynchidae* (*Belonorhynchus* and *Saurichthys*) in the teleosts, and named them as the earliest members of the group. The second is Kner (1867), who suggested that *Furo* (= *Eugnathus*, Jurassic), *Ptycholepis* (M. Trias – Jurassic) and *Pholidophorus* (M. Trias – L. Cretaceous) might be teleosts.

Darwin cited Lütken's and/or Kner's opinions with approval, as if they helped his case. But these opinions were no more than expressions of belief: in none of the fishes named had teleostean characters (of the caudal skeleton or vertebral column, for example) been demonstrated. Subsequent work has found merit in only one of the suggestions, that *Pholidophorus* should be included in the Teleostei. The genus *Pholidophorus* has since been broken up into several genera (Brough 1939, Woodward 1941, Nybelin 1966, 1974, Patterson 1973, 1975, Griffith 1977), and certain better-known species have been found uniquely to share many osteological features with teleosts (Patterson 1977). My own current opinion is that the Teleostei are best characterized, as Heckel (1850) suggested, by the presence of uroneurals. By this criterion, the earliest teleosts are late Triassic pholidophorids. Other late Triassic fishes (pholidophorids, ichthyokentemids; Griffith 1977, Zambelli 1975, 1978, 1980, Nybelin 1974) are assigned to the Teleostei not because they have uroneurals (the caudal skeleton is unknown in detail), but because they show other teleostean features, such as two supramaxillae, or show close phenetic resemblance to fishes known to possess such features. As a possible middle Triassic teleost (pholidophorid), Griffith (1977) lists *Prohalecites* sp. *Prohalecites* Deecke, 1889 was erected for late Triassic species assigned to *Pholidophorus* by Bellotti (1857) and Kner (1866). Woodward (1895: 489) referred to these as 'indeterminable immature Triassic fishes', but Alessandri (1910) argued that their size range (20–45 mm) was too great for them all to be immature, and that the specimens were sufficiently numerous and distinct to represent a good species. These remarks referred to specimens from Perledo, now thought to be of late rather than middle Triassic age, but *Prohalecites* also occurs at Besano (Brough 1939, BM(NH) specimens), which is middle Triassic. My own examination of these middle Triassic specimens has produced nothing conclusive: they are very small; they have, as Woodward said, a larval look; and they are none too well preserved. They look like pholidophorids, but I can see none of the characters that I would regard as decisive (structure of snout, epineurals, uroneurals, for example).

Thus today, as in Agassiz' and Darwin's time, the question 'which are the earliest teleosts?' can only be answered with an opinion. Opinions about the interpretation of particular fossils are less important than opinions about the characteristics of taxa like Teleostei. For a fish, fossil or Recent, can only be recognized as teleostean by recognizing teleostean characters, and the characters necessary to make a teleost are also a matter of opinion, not of fact. For instance, at one time (Patterson 1967, 1968a) I defined Teleostei by the presence of a single centrum supporting the first two hypurals, and of uroneurals extending forwards onto the pre-ural centra: this definition supported the consensus that leptolepids are teleosts and pholidophorids are not, so that teleosts first appear in the early Jurassic, as Heckel (1850) and Pictet (1858) said. I have changed my mind, and now (Patterson 1973, 1977) include in the Teleostei not only the pholidophorids, but pachycormids, aspidorhynchids, and any other fossil group which exhibits at least one character which is otherwise exclusively teleostean, implying that it is more closely related to teleosts than to any other Recent group. My change of mind was not owing to new finds of fossils, for the fishes we are arguing about (leptolepids, pholidophorids, *Prohalecites*, etc.) were all known in pre-Darwinian times. Instead, it was

because I accepted Hennig's arguments (1966, 1969) about the meaning of relationship and the distinction between monophyletic and paraphyletic groups (or, as I would now put it, between natural, characterizable groups and unnatural, uncharacterizable groups). For to draw an arbitrary line separating teleosts from non-teleosts, as is done when leptocephalids are included in Teleostei and pholidophorids are not, is to relegate pholidophorids to a paraphyletic group, characterizable only by absences of teleostean features, and absences are not characters.

So discussions about the earliest members of Teleostei, or any other taxon, concern the earliest occurrence of characters rated as diagnostic of that taxon. A familiar example is the question of the earliest mammals. Specialists agree (e.g. Lillegraven, Kielan-Jaworowska & Clemens 1979, Kermack, Mussett & Rigney 1981) that the earliest mammals are late Triassic or early Jurassic (cf. teleosts), but in phylogenetic diagrams (e.g. Carroll 1969 : fig. 1, Hopson & Crompton 1969 : fig. 1) the mammalian lineage is shown as distinct since the Carboniferous. The 'non-mammalian' members of this lineage, the mammal-like reptiles, or reptile-like mammals, are placed in uncharacterizable (paraphyletic) groups – Synapsida, Therapsida, etc. – and discussions of the origin of mammals concern a man-made problem, the appearance of one or more arbitrarily selected characters. Hennig (1969) gives a full discussion.

General principles

Agassiz (1833–44, 1859) derived two general principles from his study of fossil teleosts and other fishes, conclusions which came to be combined as one, the 'three-fold parallelism'. One conclusion was that there is a parallelism between ontogeny and the palaeontological history of a group, features which appear early in ontogeny appearing early in the fossil record, and features which appear late in ontogeny appearing late in the record. The second conclusion was that there is a parallelism between the fossil record and the natural system, characters of groups of high rank appearing earlier in the record than characters of subordinate groups (for example, 'the earliest fishes are rather the oldest representatives of the type of Vertebrata than of the class of Fishes, and that this class only assumes its proper characters after the introduction of the class of Reptiles upon the earth' – Agassiz 1859 : 166). Such principles, and diagrams like Fig. 1, seem ready-made for evolutionists, yet Darwin steered clear of the three-fold parallelism in *The Origin*. On the parallelism between ontogeny and the fossil record, he wrote (1859 : 338) 'I must follow Pictet and Huxley in thinking that the truth of this doctrine is very far from proved. Yet I fully expect to see it hereafter confirmed . . . For this doctrine of Agassiz accords well with the theory of natural selection'. And again (1859 : 449) 'Thus community of embryonic structure reveals community of descent . . . we can clearly see why ancient and extinct forms of life should resemble the embryos of their descendants, our existing species. Agassiz believes this to be a law of nature; but I am bound to confess that I only hope to see the law hereafter proved true'. I assume that the reference to Pictet in the first quotation is to his textbook (1853), whereas that to Huxley is to his 1855 paper criticizing 'the Progression theory' which, he wrote, 'resolves itself very nearly into a question of the structure of fish-tails . . . upon which so much stress has been laid by Prof. Agassiz.' Huxley's criticism concerns the structure and development of the tail in Recent teleosts; so far as it is not a play on words and their definition, I believe it is mistaken.

Darwin's caution about the three-fold parallelism was not matched by later evolutionists. The parallelism between ontogeny and palaeontology, which Darwin resisted using as evidence for his doctrine, was taken up with so much enthusiasm by Haeckel (1866) that the law now bears his name, rather than Agassiz' (cf. Hyatt 1894 : 390).

Huxley took up the three-fold parallelism in his two presidential addresses to the Geological Society (1862, 1870), on the theme of the fossil record and its bearing on theories of transformation. The first of these addresses was a pessimistic stock-taking, written in the

terms of the three-fold parallelism; the second was a more optimistic progress report. In both, Huxley used the teleost *Beryx* as evidence for lack of change: 'In what respect is the *Beryx* of the Chalk more embryonic, or less differentiated, than *Beryx lineatus* of King George's Sound?' (1862: li; 'embryonic' and 'differentiated' refer to the non-palaeontological terms of the three-fold parallelism); and 'off the coast of Portugal, there now lives a species of *Beryx*, which doubtless, leaves its bones and scales here and there in the Atlantic ooze, as its predecessor left its spoils in the mud of the sea of the Cretaceous epoch' (1870: xlv). In drawing attention to 'persistent types' like *Beryx*, Huxley's intention was to support Darwinism, which allowed both persistence and change, against Agassizian creationism, which allowed change but not persistence. In the text accompanying the original of Fig. 1, Agassiz wrote 'having recognized that the species of each formation are always different from those of other epochs, I have drawn the lines separating the geological horizons across all the ascending lines of the families to show that the genealogical development of the species is repeatedly interrupted' (1844: 170). In other words, 'species do not pass insensibly from one to another, but appear and disappear suddenly, without direct connection with their precursors . . . All these species have a fixed time of appearance and disappearance; their existence is likewise limited to a determined period' (1844: 172).

Agassiz' theory is open to test here, for if it could be shown, for example, that a Recent species of teleost existed in the Cretaceous, Agassiz would be wrong, and Darwin, whose theory permitted such things, might be right. Hence Huxley's appeal to *Beryx*. Agassiz was prepared for such appeals, arguing that species which appeared to range through more than one period were due to inadequate systematics: 'The number of the species, still considered as identical in several successive periods, is growing smaller and smaller, in proportion as they are more closely compared' (Agassiz 1859: 156). Huxley, in comparing Chalk and Recent *Beryx*, proposes that they are the same, whereas Agassiz believes that close comparison will show them to be different. At first, it seemed that Huxley was right, for following Woodward's (1902) account of the Chalk species *Hoplopteryx lewesiensis* (previously placed in *Beryx*), Regan (1911) transferred the Australian *Beryx lineatus* (one of the Recent species mentioned by Huxley) to the Cretaceous genus *Hoplopteryx*. But more detailed study of *Hoplopteryx* (Patterson 1964) showed that it differs from Recent Berycidae in many ways, and is better placed in the family Trachichthyidae. Subsequent work on Recent beryciform fishes (Rosen 1973, Zehren 1979) has shown that the relationship between Berycidae and Trachichthyidae is not particularly close, that the Trachichthyidae may not be a monophyletic group, and that the characters relating the Cretaceous *Hoplopteryx* to Recent trachichthyids are probably all primitive for the group. Rosen (1973) called trachichthyoids. Thus here Huxley was wrong and Agassiz was right. Huxley's original question (1862) was 'in what respect is the *Beryx* of the Chalk more embryonic, or less differentiated, than *Beryx lineatus* . . . ?' One answer might be that in Recent berycids the caudal skeleton contains a compound element representing the fused first pre-ural and first and second ural centra, and the stegural; and the third and fourth hypurals are fused (Zehren 1979). In the Chalk *Hoplopteryx* the second ural centrum, the stegural and the third and fourth hypurals are all separate (Patterson 1968b). Since there is evidence that these parts of the caudal skeleton fuse during ontogeny in beryciforms, *Hoplopteryx* is 'more embryonic, or less differentiated' than Recent berycids.

Sauvage (1869), reviewing the fossil record of teleosts, wrote that 'Agassiz' first great law [that teleosts do not appear until the Cretaceous] seems to be true in general, and if Jurassic teleosts exist, they are relatively very rare. But the law of the successive development of organisms in accordance with embryonic types, a law laid down with assurance by Agassiz and by Vogt [Carl Vogt, Agassiz' assistant or student, 1839-44], is found wanting completely, so far as the leptolepids are concerned. These Jurassic teleosts are closer to the Halecoïdes than to any other group, and as Pictet & Humbert pointed out [(1866a)], in their monograph on the fishes of Lebanon, the herrings and salmons represent "in a way the archetype of the class, and possess its normal characters to the highest degree". By his use of this quotation from Pictet & Humbert (the paper that Darwin read with such enthusiasm),

Sauvage seems to imply that the leptolepids refute Agassiz' parallelism between ontogeny and palaeontology by conforming to his parallelism between systematics and palaeontology. Darwin and Huxley did not comment directly on this second aspect of the three-fold parallelism. This may have been due to the contrast between the Darwinian and Agassizian view of the ontological status of the natural system. To Agassiz, the elements of the natural system – species and higher taxa – were real: 'Species do not exist in nature in a different way from the higher groups' (Agassiz 1859 : 8); 'For many years past I have lost no opportunity of urging the idea that while species have no material existence, yet they exist as categories of thought, in the same way as genera, families, orders, classes and branches of the animal kingdom. Darwin's fundamental idea, on the contrary, is that species, genera, families, orders, classes and any other kind of more or less comprehensive divisions among animals do not exist at all, and are altogether artificial . . . If species do not exist at all, as the supporters of the transmutation theory maintain, how can they vary?' (Agassiz 1860*b* : 142–3). Darwin's answer to that last point was 'How absurd that logical quibble . . . As if anyone doubted their [i.e. species] temporary existence' (F. Darwin 1887, 2 : 333).

To Darwin, then, species were temporary, arbitrary segments of a continuum (Cracraft 1979). Darwin's view of higher taxa is more controversial; some believe that he regarded them as real, others that he thought higher taxa were also arbitrary chunks of a continuum (Ghiselin 1969, Hull 1973, Nelson 1974). By the 1860s, Huxley's view of species was presumably the same as Darwin's. On higher taxa, he wrote 'there may be as many classifications of any series of natural . . . bodies, as they have properties or relations to one another . . . so that . . . it might be more proper to speak of a classification than of the classification of the animal kingdom . . . Now, a morphological classification . . . answers the purpose of a *memoria technica* . . . But there is a second and even more important aspect . . . it expresses, firstly, a generalization . . . and, secondly, a belief . . . The generalization is that, in nature, the structures mentioned [in the definition of a group] are always found associated together: the belief is, that they always have been, and always will be, found so associated' (Huxley 1864 : 1–3, 1869 : 1–3). To Huxley, higher taxa are what Kitts (1977) called 'strictly universal hypotheses about character state association' – they seem to be as timeless and changeless as Agassiz' 'categories of thought' and far less real than Darwin's 'chunks of the genealogical nexus' (to use Ghiselin's 1969 phrase). Yet we should remember that the genealogical nexus has attributes of a category of thought, for it is not directly observable. Huxley's description of taxa does demand that they be definable, i.e. that they have characters.

Against this background, what of Sauvage's and Pictet & Humbert's appeal to leptolepids and Halecoïdes against the three-fold parallelism? The problem is that a group containing herring and salmon (Halecoïdes), and omitting, for example, esocids (cf. Fig. 1), is an ideal subject for talk of archetypes, since the group is uncharacterizable. It is an instance of what Eldredge & Cracraft (1980) call a 'not-A group', or what I prefer to call a non-group (Patterson 1980): one defined only by the absence of characters, and therefore lacking an empirical definition, or any existence in nature. The same seems to be true of leptolepids: they too are definable only by lack of the characters of Recent teleosts, with the added disadvantage that few are well enough known even to demonstrate these deficiencies. The conclusions drawn from comparison of two non-groups are unlikely to impinge on any general principle.

What, then, of Agassiz' three-fold parallelism? To him, at least, it was based on empirical observation, so perhaps he saw the fact of evolution without realising the implication. Jordan (1905, 1 : 381) quotes Agassiz in old age, referring to the time of his work on fossil fishes, saying 'At that time I was on the verge of anticipating the views of Darwin, but it seemed to me that the facts were contrary to the theories of evolution. We had the highest fishes first.' Here Agassiz seems to deny the three-fold parallelism, and in his posthumous criticism of Darwinism he wrote (1874 : 11; also Hull 1973 : 443) 'Let us look now at the earliest Vertebrates, as known and recorded in geological surveys. They should, of course, if there is any truth in the transmutation theory, correspond with the lowest in rank or

standing. What then are the earliest known Vertebrates? They are Selachians (sharks and their allies) and Ganoids (garpikes and the like), the highest of all living fishes, structurally speaking.' In a footnote, Agassiz explains 'I use the terms low and high, throughout, in the zoological sense; with reference to specialization of structure, as comparative anatomists understand it'. In 1860 (1860a : 233) Agassiz said 'the earliest fishes are among the most perfect of their class, and have many reptilian characters'. Questioned about the apparent conflict between this statement and the parallel between embryology and palaeontology, and about the meaning of 'perfection', Agassiz replied that he took perfection 'to mean an embodiment of the highest combinations, the most complex representation of life. The embryo fish presents features of its type superior to those of the adult fish; the tendency to specialization increases with its growth, and the animal at last becomes only a fish, losing its embryonic type of the higher vertebrates. As a generalization or philosophic conception, the vertebrate egg is superior to man himself, inasmuch as it embodies all that may be produced from it.' If this is not mumbo-jumbo, it seems to be an attempt to reconcile von Baer's (1828) law, which Agassiz had previously rejected (Gould 1977 : 64), with a three-fold parallelism modified by equation of 'generalized' (in von Baer's sense) with 'high'. Darwin wrote 'Never use the words higher and lower' in the margin of his copy of *Vestiges of the Natural History of Creation* (Burrow 1968 : 33); and Gill (1872 : xxxvi) wrote 'Perhaps there are no words in science that have been productive of more mischief and more retarded the progress of biological taxonomy than those words, pregnant with confusion, HIGH and LOW, and it were to be wished that they might be erased from scientific terminology. They deceive the person to whom they are addressed; they insensibly mislead the one who uses them.'

To sum up Agassiz' achievement with respect to fossil teleosts, his production of Fig. 1, having initiated the investigation of fossil fishes virtually from scratch, is extraordinary. That he was mistaken in attempting to characterize Cycloidei and Ganoidei is a minor blemish, in part a consequence of the difficulty of characterizing groups with extinct members, and of assigning inadequately known fossils to groups, problems that are still with us. That Agassiz produced Fig. 1 without reference to, or belief in, theories of transformation is a salutary response to those who use such diagrams, with the addition of some dotted lines, as an expression or exposition of evolution. If Fig. 1 were redrawn using the current classification of teleosts, the pattern it reveals, of a sudden influx in the late Cretaceous and early Tertiary, would still exist. In a wider context, Agassiz first derived the three-fold parallelism from his work on fossil fishes. At first, he saw it as a powerful theory, offering a research programme uniting the whole of systematics and palaeontology with embryology. Later, like so many other theories, the three-fold parallelism seems to have degenerated as Agassiz added to it such things as 'prophetic types' and 'synthetic types' (1859), and as he maintained his opposition to any modification of the four Cuvierian basic plans in the animal kingdom. Through his adherence to such views, by the 1870s Agassiz had become what Hull (1973 : 449) called 'a living fossil'. Yet the three-fold parallelism had a glorious future, after it was taken up by Haeckel (Gould 1977), and its interest is not yet exhausted (Nelson 1978).

Darwin's (1859, 1872) comments on fossil teleosts, though more agreeable to modern sensibilities than Agassiz', show up the problems with his own theory as plainly as do Agassiz'. Whether teleosts appeared suddenly in the Cretaceous, as Agassiz supposed, or more gradually in the Jurassic or Triassic, as Heckel, Kner and Lütken supposed, are questions that can only be approached through systematics – characterization of groups – a field in which opinion and its substitute, authority, are still paramount. As Darwin's comments imply, no opinion or authority on such questions could run counter to his theory, for there is always the appeal to imperfection of the record, or to development within a 'perfectly enclosed basin, in which any great group of marine animals might be multiplied' (1859 : 306). Transformation offers an even more all-embracing research programme than the three-fold parallelism.

Huxley's comments on fossil teleosts were more factual than Darwin's. Where Huxley attempted direct criticism of Agassiz, as with the ontogeny of the teleost caudal skeleton and Cretaceous *Beryx*, Agassiz seems to have been right and Huxley wrong. Huxley's

attempt to extend the fossil record of teleosts into the Palaeozoic, though now virtually forgotten, initiated what later became common practice in palaeontology – driving lineages back into the past without regard to adequate characterization of the group (lineage) by comparative analysis of its living members. Hence evolutionary palaeontologists' predilection for supposed demonstrations of polyphyly. The 'breakdown in logic' (Nelson 1969 : 528) behind such proposals has only recently been appreciated. Together with that appreciation, I see a revival of interest in Agassizian ideas like the three-fold parallelism (e.g. Nelson 1978) and the adequacy of the fossil record in demonstrating the sudden, rather than gradual, appearance of species and groups (e.g. Stanley 1979, Gould 1980).

The generalizations that Agassiz drew from fossil teleosts may seem to us mistaken, or tainted with outdated metaphysics. Yet they can only be favourably compared with the ideas of his British counterpart, Owen, whose general conclusion on fossil teleosts was 'that those species, such as the nutritious cod, the savoury herring, the rich-flavoured salmon, and the succulent turbot, have greatly predominated at the period immediately preceding and accompanying the advent of man, and that they have superseded species which, to judge by the bony Garpikes (*Lepidosteus*), were much less fitted to afford mankind a sapid and wholesome food' (Owen 1860 : 151). These seem to be the words of a pious victualler.

Agassiz and Darwin viewed the fossil teleosts in a context wider than the kitchen. To Darwin, they were one aspect of that 'mystery of mysteries', the origin of species, for which gradual transformation provided a material explanation. To Agassiz, the origin of species was no more mysterious than the observable transformations of ontogeny. He came to regard ontogeny as the overriding mystery (the only one worthy of the name evolution; 1874 : 92), and the only source of material explanations in systematics and palaeontology. That point of view still has advocates (Nelson 1978, Patterson in press).

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